

<https://helda.helsinki.fi>

---

## Epigenetic variation as a new plant breeding tool : A review

Alfalahi, Ayoob Obaid

2022-11

---

Alfalahi , A O , Hussein , Z T , Khalofah , A , Sadder , M T , Qasem , J R , Al-Khayri , J M , Jain , S M & Almehemdi , A F 2022 , ' Epigenetic variation as a new plant breeding tool : A review ' , Journal of King Saud University - Science , vol. 34 , no. 8 , 102302 . <https://doi.org/10.1016/j.jksus.2022.102302>

---

<http://hdl.handle.net/10138/352454>

<https://doi.org/10.1016/j.jksus.2022.102302>

---

cc\_by\_nc\_nd

publishedVersion

---

*Downloaded from Helda, University of Helsinki institutional repository.*

*This is an electronic reprint of the original article.*

*This reprint may differ from the original in pagination and typographic detail.*

*Please cite the original version.*



## Review

## Epigenetic variation as a new plant breeding tool: A review

Ayoob Obaid Alfalahi <sup>a</sup>, Zeyad Tariq Hussein <sup>b</sup>, Ahlam Khalofah <sup>c,\*</sup>, Monther Taha Sadder <sup>d</sup>,  
Jamal Ragheb Qasem <sup>d</sup>, Jameel Mohammed Al-Khayri <sup>e</sup>, Shri Mohan Jain <sup>f</sup>, Ali Fadaam Almehemdi <sup>g</sup>

<sup>a</sup> Department of Plant Protection, College of Agriculture, University of Anbar, Anbar, Iraq

<sup>b</sup> Department of Field Crops, College of Agriculture, University of Anbar, Anbar, Iraq

<sup>c</sup> Department of Biology, College of Science, King Khalid University, Abha, Saudi Arabia

<sup>d</sup> Department of Plant Protection, Faculty of Agriculture, University of Jordan, Amman, Jordan

<sup>e</sup> Department of Agricultural Biotechnology, College of Agriculture and Food Sciences, King Faisal University, Al-Ahsa, Saudi Arabia

<sup>f</sup> Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland

<sup>g</sup> Department of Conservation Agriculture, Center of Desert Studies, University of Anbar, Anbar, Iraq



## ARTICLE INFO

## Article history:

Received 11 May 2022

Revised 24 August 2022

Accepted 29 August 2022

Available online 5 September 2022

## Keywords:

Acetylation

Chromatin remodeling

DNA methylation

ncRNA

## ABSTRACT

Epigenetic variations are inherited or uninherited effects that occur beyond the DNA sequence of an individual. However, DNA sequence has a critical role in shaping epigenetic variation. The great diversity of epigenetic markers confers an advantage of various uses without interrupting its highly environmental independence. The epigenetic effects are highlighted by many vital events, especially the regulation of gene expression in hybrid vigor and inbreeding depression, even in the absence of genetic diversity. However, various stress genes can include many repeats that undergo alternately methylation and demethylation states to regulate gene expression positively or negatively. After all the arguments raised on the genetic basis of hybrid vigor in its both traditional and molecular aspects, the term “epigenome” strongly emerged as one of the main causes of performance deviation among offspring. These include both histone and DNA biochemical modifications, which play a key role during successive stages of development and differentiation in addition to the regulation of gene expression in response to biotic and abiotic stresses. Evidence has shown a correlation between unique DNA methylation and heterosis in many plant species as well as between inbreeding and the sharp decline in fitness of most naturally cross-pollinated species. Although detailed molecular mechanisms laying behind many of these plant breeding aspects remain little understood, epigenetics has provided some explanations.

© 2022 The Author(s). Published by Elsevier B.V. on behalf of King Saud University. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## Contents

1. Introduction	2
2. Histone acetylation	2
3. Non-coding RNA	3
4. Chromatin remodeling	3
5. DNA methylation	4
6. DNA methylation effects on hybrid vigor	4
7. Inbreeding and DNA methylation	5
8. Modulation of stress through epigenetic regulation	7

\* Corresponding author.

E-mail address: [aalshayeed@kku.edu.sa](mailto:aalshayeed@kku.edu.sa) (A. Khalofah).

Peer review under responsibility of King Saud University.



Production and hosting by Elsevier

<https://doi.org/10.1016/j.jksus.2022.102302>

1018-3647/© 2022 The Author(s). Published by Elsevier B.V. on behalf of King Saud University.

This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

9. Stress mitigation via epigenetic memory . . . . .	7
10. Genetic and epigenetic aspects of Somaclonal variations . . . . .	7
11. Transposable elements and epigenetic effect. . . . .	8
12. In vitro culture influence on epigenetic . . . . .	8
13. Regulation of reproductive plant development by epigenetics. . . . .	8
14. Reversal of flower color in transgenic <i>petunia</i> under field conditions . . . . .	9
15. Active compounds as epigenetic modulators . . . . .	9
16. Conclusions and recommendations. . . . .	9
17. Competing interests statement . . . . .	9
Declaration of Competing Interest . . . . .	9
Acknowledgment . . . . .	9
References . . . . .	9

## 1. Introduction

Traditional plant breeding is focused on capturing and gathering many variable and desirable alleles for possible improvement of traits of interest, in addition to plant efficiency in using limited natural resources (Postnote, 2017; Kaiser et al. 2020). The development of modern molecular tools facilitates achieving breeders' goals (Sadder et al. 2014). Plant breeding goals can be categorized into two major aspects; namely the improvement of agronomic traits (including yield and quality components) and stress mitigation including various abiotic and biotic factors (Hamany Djande et al. 2020).

Until recently, genetic variation that commonly points to the heritable variation of genetic information of individuals and populations was thought to be the only responsible factor for revealing phenotypic traits (Goulet et al., 2017). However, researchers discovered yet another source of variation in view of various traits among individuals within the same species, which has no direct correlation with DNA polymorphisms. These newly discovered variations which coined the term "epigenetics" has received considerable attention to better understand their stability through successive generations (Cavalli and Heard, 2019; Springer and Schmitz, 2017; Zenda et al. 2021).

The heritable or reversible changes in gene expression happen at a level higher than that of the nucleotide sequence. In other words, it is not attributed to alterations in the type and/or sequences of DNA nucleotides (Alvarez-Venegas et al. 2003; McKeown and Spillane, 2014; Liu et al. 2017b).

Genetic and environmental variations and their interactions naturally induce phenotypic variations. Altered phenotypic traits may be resulting from an identical genetic structure and such alterations result from identical alleles acting in different ways in response to biotic or abiotic stress (Fortes and Gallusci, 2017; Zhi and Chang, 2021). Naturally characterized epialleles are relatively few, consequently, the role of epigenetic variation in revealing large phenotypic alterations is still vague (Springer and Schmitz, 2017). Epigenetic changes usually participate with a variety of chromatin marks, such as cytosine methylation, modifications of histone tail, chromatin remodeling and non-coding RNAs (Saleh et al. 2008; Rajewsky et al. 2017).

The objective of this communication is to briefly introduce epigenetic variations as a breeding tool that may support traditional genetic variation in widening the genotypic gap, hence improving the opportunity for plant breeders to achieve hybrid vigor in the desired attributes.

## 2. Histone acetylation

Nucleosome is a 147 nucleotide (nt) of DNA wrapped tightly around a core of eight polymer histones considered the basic unit of chromatin. The described octamer consists of two of each of the

following molecules: H2A, H2B, H3 and H4. Histones are highly positively charged proteins, including 24 amino acids of lysine and arginine. As DNA can be methylated, histones can be subjected to numerous posttranslational modifications, e.g., acetylation, methylation, and phosphorylation (Demetriadou et al., 2020; Grabsztunowicz et al., 2017).

Histone acetylation is being widely studied as a major form of epigenetic modifications in addition to DNA methylation. It is obvious that the core histones are acetylated in a reversible manner (Liu et al. 2017b), service in posttranslational modifications, like acetylation, methylation, ubiquitination, phosphorylation and ribosylation of adenosine diphosphate (ADP). Surprisingly, many of the epigenetic mechanisms operate cooperatively via organizing the work of each other to regulate gene expression during cell differentiation. This "fine-tuning" mode of action would guarantee a precise operating system, such as in histone deacetylation which helps in the maintenance of DNA methylation (Blevins et al., 2014; Lee et al. 2017).

In the last two decades, DNA methylation was proved to be a major component of the plant epigenome; likewise, histone acetylation was recently investigated as another major player in epigenetics (Shi et al. 2019). These claims created compelling arguments for lysine's acetylation in histone tails, which is often correlated with an increased expression of accompanied genes (Xiao et al. 2017). It should be noted here that DNA acetylation involves the addition of acetyl (CH<sub>3</sub>COO<sup>-</sup>) group to the NH<sub>3</sub><sup>+</sup> group of lysine amino acid, whereas histone deacetylation eradicates the acetyl groups (Boycheva et al., 2014).

Advancement in epigenetic research enables understanding of the function and regulation of histone acetylation in plants, which delivers more accurate assessments as compared to inhibitors. In maize, several copies of histone acetyltransferases and histone de-acetyltransferases have been biochemically characterized (Zhou et al., 2017; Kopytko et al., 2020). However, it is not clear how chromatin structure is modulated by different histone acetylation states, the most common scenario is deduced from the crystal structure of nucleosomes in which non-acetylated tails of histone are available to interact with nearby nucleosome beads and moderate higher-order chromatin wrapping (De Ioannes et al. 2019). Therefore, this suggests the norm of action of histone deacetylases; on the contrary, histone acetyltransferases would moderate chromatin relaxation (Boycheva et al., 2014; Peng et al., 2017).

An important histone modification, attracting great attention, is the acetylation of protected lysine  $\alpha$ -amino acid, particularly in amino-terminal tails. The competitive effect of either HAT or HAC histone acetyltransferase enzymes against histone deacetylase (HDA) enzymes determines histone acetylation levels (Ma et al. 2013; Wang et al. 2014). Dozens of HATs, HACs and HDAs have been characterized in plants, which have critical roles as biotic and abiotic stimulants and as functional regulators in normal developmental processes (Peng et al., 2017; Zhao and Zhou, 2012).

In plants, like most eukaryotes, HAT-A and HAT-B are the two major types of histone acetyltransferase enzymes ( Liu et al. 2017b). The HAT-A enzymes have special importance since occupying the nucleus and operate to acetylate core histones which have been integrated into the chromatin; therefore, they are involved in controlling gene expression ( Boycheva et al., 2014; Giaimo et al., 2019 ).

Certain changes in histone acetylation were found to be related to DNA replication at the cytological level rather than to their transcriptional activity ( Vergara and Gutierrez, 2017 ). Such changes have been identified by using acetylated histone antibody isoforms (Li et al., 2017). During the cell life cycle, there are various oscillations with histone acetylation which are controlled by HAT-B enzymes (Class 2 of histone acetyltransferases), ( Yongfeng et al. 2019). Free cytoplasmic histone (H4 or H3) would initially be acetylated by HAT-B enzymes, enter the nucleus to be deposited into recently replicated chromatin ( Yang et al., 2011a,b). According to single nucleotide homology, there are three groups of plant HDAs: the first named reduced potassium dependency 3 (RPD3)/HDA1, while the second is histone deacetylase 2 (HD2) and silent information regulator 2 (SIR2) is the third type ( Ma et al. 2013; Wang et al. 2014 ).

### 3. Non-coding RNA

The tremendous revolution in the epigenomic era has provided researchers with invaluable findings prompting a continuous revision of plant genetics. In general, the eukaryotic genome is not simple, and over time, accumulated evidence has endorsed such complexity ( Jin et al. 2017). Absolute scientific facts were brought back to the discussion table. One of these abolished statements restricts transcripts to be exclusively derived from protein-coding domains ( Berretta and Morillon, 2009 ). Surprisingly, the encoding proteins come from a tiny portion (2–25 %) of the total genome space (Liu et al. 2015 ).

Although non-coding RNAs (ncRNAs) do not end up with manufactured proteins, as usual, their regulatory role for various biomechanics cannot be overlooked ( Liu et al. 2017a). Several ncRNAs have been suggested as effective tools in directing cell division and differentiation, as well as regulating plant response to environmental stresses at transcriptional and posttranscriptional levels ( Cavalli and Heard, 2019; Matsui et al., 2013; Sunkar et al., 2012).

Non-coding RNAs can be organized into two classes, the well-studied small ncRNAs (sncRNAs), which consist of less than 200 nt and long ncRNAs (lncRNAs), which consist of more than 200 nt, the latter being less studied ( Zhang and Chen, 2017).

The sncRNAs have very small molecular weights, and they have been studied extensively for decades in both plants and animals (Bhatia et al. 2017). There are two main groups of plant sncRNAs, short interfering RNAs (siRNAs) and microRNAs (miRNAs). The two groups differ in their genetic origin and their natural consequence of regulation ( Rajewsky et al. 2017 ).

Typically, siRNA refers to exogenous double-stranded RNA (dsRNA) that is brought from outside of the cell, whereas the endogenous stem-loop non-coding RNA produces the single-stranded miRNA ( Guleria et al. 2011 ). The RNase Dicer-Like will be responsible for processing each of the three non-coding RNAs, miRNA and siRNA, to be transported in the next step out of the nucleus to bind with Argonaute (AGO) proteins into the cytoplasm and integrate them to shape the RNA-induced silencing complex (RISC) (Prathiba et al. 2017; Setten et al. 2019 ), which in many occasions regulates the expression of the target gene at a post-transcriptional level ( Carthew and Sontheimer, 2009; Layton et al., 2020; Vaucheret et al., 2006 ). The mobility of sncRNA mole-

cules inside the organism may serve to ease gene silencing in different plant cells and tissues ( Sarkies and Miska, 2014). In addition, sncRNAs have been found to play a critical role in regulating DNA methylation, histone modifications and gene silencing, consequently, controlling the transcriptional system in living organisms (Holoch and Moazed 2015).

During the past decades, plant miRNAs have been intensively studied. Although they have a small molecular size (21–24 nt), miRNAs roles are particularly important in the regulation of various biological processes through targeted mRNA repression, either by degradation or translation inhibition ( Wu, 2013). To fulfill their function ideally, miRNAs have a complementary sequence, which closely matches their respective mRNAs targets. The binding of miRNAs to their complementary sequences confers their ability to regulate gene expression, which is more advanced in plants as compared with their counterparts in animals, where just limited regions of miRNA are available ( Narjala et al. 2020 ); therefore, they have a restricted complementary action ( Xu et al. 2017). Recent biochemical and genetic evidence indicates that many miRNAs could regulate their own targets during translation ( Bordersen et al. 2008; Prathiba et al. 2017 ). They have key functions in controlling plant differentiation, a transition from vegetative to reproductive phase, morphogenesis of reproductive organs, phytohormone stimulation, stress-response regulation and they may even control the pathway of their biogenesis ( Zhao et al. 2017





















